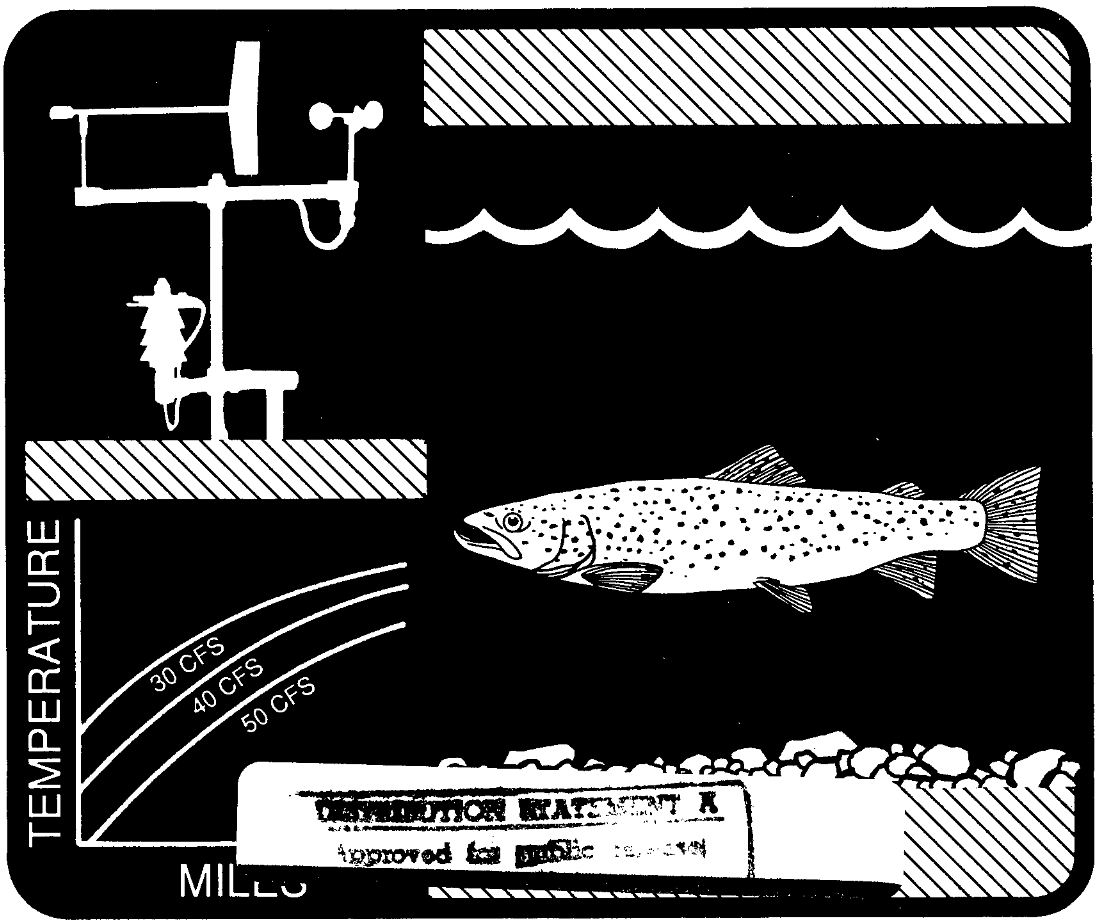
Evaluating Temperature Regimes for Protection of Brown Trout



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By Carl L. Armour

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Abstract. Geographic distribution and population success of brown trout (*Salmo trutta*) are affected by temperature regimes. Concepts are presented for evaluating alternative temperature regimes for brown trout based on published temperature information and professional judgment. Temperature information from the literature is included for spawning runs, spawning, egg and larval development, growth, and other subjects. The objective is to aid biologists in evaluating alternative temperature regimes so as to select those that will protect and enhance environmental quality for brown trout.

Key words: Alternative temperature regimes, brown trout, *Salmo trutta*, water temperature.

The brown trout (*Salmo trutta*) is not a native species. It was introduced to North America in 1883 and is distributed widely in the United States and Canada (Lee et al. 1980). The brown trout is an important sport fish, and there is public demand for protecting and improving its habitat. Water temperature is one of several environmental factors affecting success of brown trout throughout its range (Fig. 1). Water temperature directly affects spawning, egg and larval development, and growth of fry and older life stages. Indirect effects of temperature include influences on food abundance, toxicity of water-borne pollutants, oxygen concentrations in water, and biochemical oxygen demand.

Temperature effects on brown trout cannot be documented completely because of complex interactions, including synergism with other variables. Nonetheless, management decisions must be made, and biologists are required to use available information and professional judgment in recommending appropriate temperature regimes. The objective of this report is to assist biologists in designing site-specific procedures for evaluating alternative temperature regimes. For example, one might want to evaluate the temperature regimes that would result from varying water releases below a reservoir. General information regarding habitat requirements for brown trout is addressed in a habitat suitability index model (Raleigh et al. 1986). Additional information on habitat requirements of salmonids in streams can be found in Bjornn and Reiser (1991).

Information in this report was compiled from the literature, including studies under natural field conditions and controlled experiments. Care should be taken in extrapolating experimental results to field situations. For example, brown trout growth is affected by temperature, other

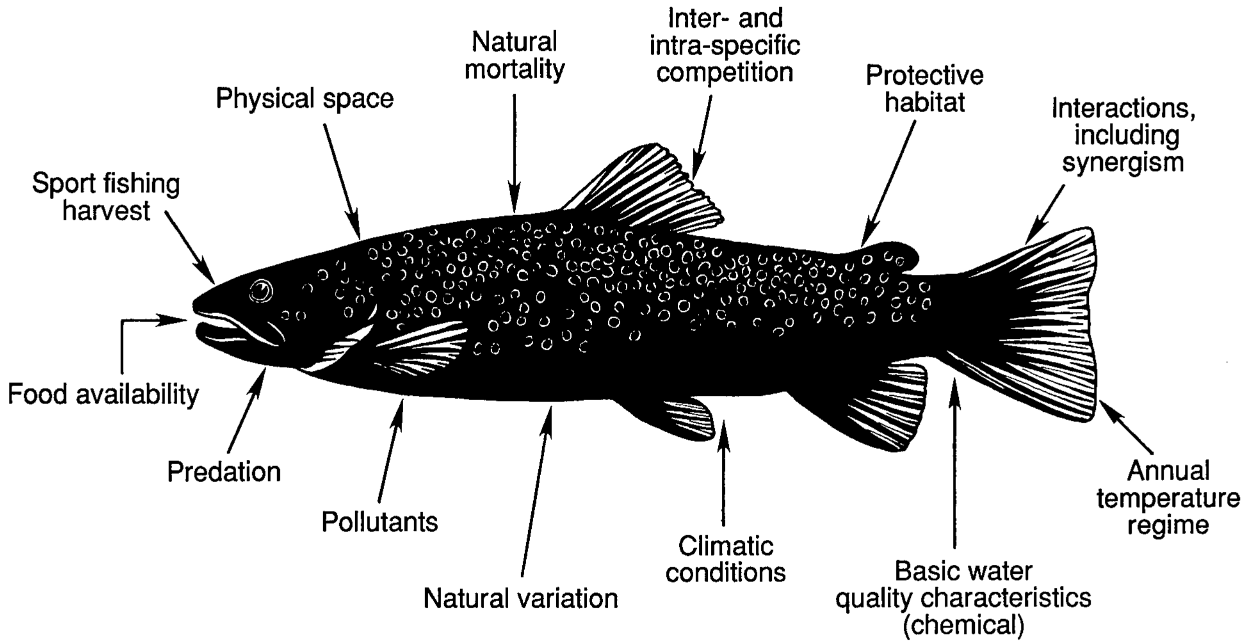

Fig. 1. Variables that affect brown trout populations.

water quality variables, and environmental factors, including food availability, whereas spawning and egg incubation success are controlled more directly by temperature. Hence, even if spawning substrate, oxygen concentration, and water quality variables other than temperature meet brown trout habitat criteria, success of egg incubation still depends on water temperature (Jungsworth and Winkler 1984).

This report does not include all possible approaches for evaluating alternative temperature regimes. Final decisions on which approaches to use should be made collaboratively with experts knowledgeable about brown trout in the geographic areas where the temperature studies will be performed.

Conceptual Approaches

Conceptual approaches for evaluating alternative temperature regimes for brown trout are similar to those for fish in general (Armour 1991), smallmouth bass (*Micropterus dolomieu*; Armour 1992a), and walleye (*Stizostedion vitreum*; Armour 1992b; Table 1). These approaches include use of simulated temperature curves and temperature envelopes for evaluating the suitability of temperature regimes for specific life stages. The temperature envelope approach requires use of a standard envelope in the U.S. Environmental Protection Agency data base (Biesinger et al. 1979; Hokanson et al. 1990). Information from throughout the range of brown trout in North America was used to develop the temperature envelopes. Temperatures for alternative regimes for specific life stages are compared with the envelope, and temperatures that fall within the envelope are assumed to be acceptable.

Armour (1991) presented methods applicable to brown trout for using experimentally derived temperature tolerance information to evaluate alternative temperature regimes. The methods pertain to estimates of maximum weekly average temperatures that should not be exceeded, short-term maximum survival temperatures, and estimation of lethality of an exposure time. Table 2 contains information for use in the computations.

Following is an example of a method that does not require the use of curves or envelopes (Table 3). Suppose that the primary concern for a site is temperatures during the incubation period, where other water quality parameters and habitat

Table 1. Brown trout temperature data compiled from literature.

Attribute	Observation[a]	Reference and fish source	Comments
Spawning			
Range was 8.9 to 12.8° C	GS	Piper et al. (1982), general observation	Reported that eggs develop well in hard water at 10.0° C
Mean temperatures ranged from 3.8 to 7.4° C	GS	Elliott (1984), Black Brows Beck, English Lake District	Mean water temperatures during egg development ranged from 3.3 to 6.7° C
Range was 6.1 to 11.1° C	F	Johnson et al. (1966), artificial spawning channel, Owens River, California	The earliest date observed for redds was 30 October compared with 11 December for the last redds observed
Peak spawning was in 6.1 to 12.8° C range	GS	Reiser and Wesche (1977), locations for observations unstated	The information was from literature sources. The authors reported that the mean temperature at first spawning was 8.3° C for Douglas Creek, Wyoming
Fertilization, incubation, and hatching			
Required 835–850 degree-days from egg deposition to emergent fry stage	E	Elliott (1988), Wilfin Beck, United Kingdom	Laboratory temperatures ranged from 5.2 to 6.6° C. Egg weight had no effect on degree-day requirements. The author (Elliott 1984) stated that fry emergence required 852 degree-days (50% hatching) at another location. A degree-day is defined as a day when temperatures are above freezing
Normal trout larvae were raised from eggs incubated at 2.8 to 13° C without high mortality	E	Gray (1928)	Observation based on constant temperatures
Eggs developed normally in water up to 10° C	GS	Markus (1962), general statement for hatcheries	After feeding begins, best growth seems to be at 12.8° C
$y = \frac{a}{(x-b)^c}$ where y = days to hatching, x = incubation temperature (° C), and a, b, and c are constants	E	Jungsworth and Winkler (1984). Adult stock was from the Lunzer Untersee River, Austria	For the Belehrádek equation, the value for a = 746, b = −0.5323, and c = 1.2233. X values were for the mean incubation temperature Experiments were conducted to derive values for the constants. For the regression equation, 99.93% of the total variance was explained ($p < 0.01\%$). The range of temperatures for the experiment was 2 to 16° C
A good proportion of eggs hatched at a range of 5 to 13° C	GS	Frost and Brown (1967), British Isles	The optimum temperature for development was 7 to 12° C. Outside the range, alevins were smaller because more yolk is used for energy requirements instead of growth
Brown trout had poor reproductive success in water with maximum summer temperatures of	F	Kaya (1977b), Firehole River, Yellowstone National Park	Gonadal maturation was impaired. In the geothermally heated part of the river, rainbow trout outnumbered brown trout by three to one. Rainbow trout reproduced

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
28.0 to 28.8° C for 5 consecutive days			successfully but spawned in the fall instead of the spring. Kaya (1978) reported that the wild rainbow trout did not seem capable of acclimating to higher water temperatures more than hatchery strains. The same limitation probably applies to brown trout. This indicates the risk of making assumptions about genetic differences of trout to tolerate higher temperatures
Equation for use in estimating hatching time in the field: $d = D/(T-T_0)$ where d = time in days after fertilization; D = degree days = 444; T = mean water temperature (° C); T_0 = threshold temperature (° C) above which hatching occurs = 0.007	E	Elliott (1984), Black Brows Beck in English Lake District	I assumed that "T" represented the mean temperature for the incubation period The equation pertains to an estimate for 50% hatching to the alevin stage. The equation was also used to estimate the duration of the alevin stage by substituting 0.031° C for T_0 and 852 for D. Throughout the study, temperatures were usually in the 4.0 to 19.0° C range required for feeding and growth, and critical limits of 0 to 25° C were not exceeded
Eggs incubated at 2.8 to 13° C will develop into normal trout larvae	E	Gray (1928), assumed to be British Isles fish	The author reported high mortality above 15° C. Specific mortality rates were not given. For eggs with transparent membranes incubated at 10° C, exposure to temperatures in the 15 to 17° C range caused hatching in a few hours. However, eggs incubated at 5° C and exposed to the same temperatures did not hatch for 3 days
Survival of eggs was less than 1% in Vibert boxes buried 15 cm in substrate and covered by 12 to 20 cm of flowing water. Causes were low water temperatures and in situ freezing of redds	E	Reiser and Wesche (1979), Daniel State Fish Hatchery, Wyoming	Twenty of 60 boxes were recovered. Eleven of the 20 boxes were within criteria defined for spawning, i.e., water depth 9 cm or more, water velocity 14–16 cm/s. The experiment was in the Laramie plains, where the mean monthly air temperatures from November to March ranged from –5.1 to 0.0° C. Freezing of substrate was attributed to effects of reduced velocity of super-cooled water
Lower limit was <1° C compared with an upper limit of about 10 to 16° C. Optimum was about 5° C,	E	Humpesch (1985), spawners were collected in Austrian waters	Results are from laboratory experiments for a range (1.4 to 15.4° C) of constant water temperature treatment. In experiments with eggs placed in gravels

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
for which hatchery success was at least 80%			in streams, maximum hatching occurred at mean temperatures of about 5° C
In the range of 2.8 to 12.0° C, the expression for time from fertilization to the median swim-up (D_3) stage in days = $bD_2 + a$, where $b = 1.660 \pm 0.103$ and $a = 5.4 \pm 10.05$. $P < 0.001$	E	Crisp (1988), used published literature to obtain data for the calculations	D_2 = days from fertilization to median hatch and $\log D_2 = b \log (T- \alpha + \log a)$, where $b = -13.9306 \pm 0.4769$, $\alpha = -80.0$, and $\log a = 28.8392 \pm 0.9206$. The equation was derived for the 1.89 to 11.24° C range (Crisp 1981). "T" would be assumed to equal mean temperature Days from fertilization to median eyed stage (Crisp 1988) = $0.455D_2 + 5.0$
Days and (degree-days) by stage	E	Grande and Andersen (1990), domesticated Norwegian brown trout	In the colder water, more days and degree-days were required to reach a stage. At swim-up, feeding was initiated

Eyed	Hatch*	Swim-up
126(195)	176(250)	204(387)
49(273)	126(406)	194(273)

*50% hatching

Attribute	Observation[a]	Reference and fish source	Comments
Growth			
3.8 to 19.5° C was the approximate range for growth	E	Elliott (1975b), assumed to be British Isles fish	Trout in the 5–281-g range were used in experiments with constant and fluctuating temperatures
Maximum energy available for growth was optimal at 13 to 14° C	E	Elliott (1981), British Isles trout	The range applied to all sizes but the scope for growth is maximal at about 18° C, where energy available for growth was less because of loss in feces and other excretions
Computed final weight (g) was inversely proportional to the annual range (about 8.5 to 17.5° C) of monthly mean temperatures and directly proportional to the mean annual temperature, about 6.9 to 12.0° C	E	Edwards et al. (1979), British Isles streams	The equation for final weight (W_t) with 95% confidence limits = $100.2 - 7.69\ (\pm 1.13)T_v + 10.1\ (\pm 1.70)\overline{T}$ where T_v = annual range of monthly mean temperatures, and $\overline{T}$ = annual mean temperature. Existing temperature data were used for the computations, and maximum rations were assumed to be available. Within the range of 11 to 13° C for T_v, there was variation in W_t. The authors speculated that differences were attributed to mean annual temperatures. For instantaneous growth (G_w) rates, actual mean rates were less than computed rates, with use of the instantaneous growth rate equation
Growth was maximum at 10 to 15.6° C	E	Pentelow (1939), British Isles hatchery fish	One- and 2-year-old trout were fed *Gammarus pulex*. Appetite increased as temperature rose to 15.6° C but dropped at higher temperatures. Between 4.4 and

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
			10.0° C, growth was proportional to amount of food consumed
Temperatures for rapid growth at constant and changing temperature environments were bimodal (7 to 9° C and 16 to 19° C)	E	Brown (1946), Midland Fishery, Nailsworth Gloucestershire	Experiments were conducted on 2-year-old fish. Surplus amounts of an unspecified kind of meat were fed to the trout
Occurred in the 3.9 to 19.5° C range, with an optimum of 13° C	E	Elliott (1975a), fish from a hatchery at Pickering, Yorkshire	Feeding was at maximum rations. Live weights of experimental fish ranged from 5 to 300 g. Temperatures were fairly constant
The mean size of brown trout ranged from 49.1 to 54.6 mm for a hypolimnion release zone (compared with a range of 57.3 to 68.1 mm in an upriver zone unaffected by coolwater release)	F	Saltveit (1990), Surma River, Norway	The data pertain to the end of the summer growth period for 1984–88. In 1987 and 1988 maximum temperatures exceeded 15° C for extended periods during the summer above the hypolimnion release zone, where temperatures never exceeded 14° C
At a 11.5° C constant temperature, there was a winter check in growth	E	Frost and Brown (1967), assumed to be trout from British waters	There was a winter and autumn check in growth, and a maximum growth period in the spring. The experiment involved exposure to artificial light for 12 h per day. The author suggested that the patterns are under control of a physiological "rhythm." I assumed that the information was for brown trout. Two-year-old fish were used in the experiment
Slow outside range of 7 to 19° C; general conclusion that growth is maximum within this range	E	Frost and Brown (1967), British Isles fish	Two-year-old brown trout grew most rapidly between 7 and 9° C and less at 11.5° C, but the average growth rate was higher between 16 and 19° C. The length of the photoperiod can be a factor affecting growth (i.e., there was a positive effect in early spring with increased day lengths). Decreased day length in fall had a negative effect
Maintenance ration (D_{main}) in mg dry weight per day = $day^{-1} = aW^{b_1}e^{b_2T}$	E	Elliott (1975b), assumed to be British Isles hatchery fish	D_{main} represents the ration that merely maintains a fish without any weight changes. The experiment usually involved use of *Gammarus pulex* as the food. D_{main} is positively correlated with water temperature. The fish for the experiment weighed 10–300 g

where a and b are constants for two temperature ranges:

	3.8–6.6° C	6.6–19.5° C
a	1.390	2.711
b_1	0.716	0.737
b_2	0.22	0.105

and W = mean weight (g)

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
Temperatures from 11.1 to 14.4° C provided rapid growth in rearing ponds	GS	Davis (1953), no reference to geographic locations	I assume that the recommended range applies to brown trout
Maximum growth was at 12° C	E	Swift (1961), British Isles hatchery brown trout	Yearlings were used in the experiment. Treatments involved fish directly from a hatchery and those that were stocked into the wild
The predicted final weight $W_t = (W_o 0.33 + G_S t)^3$, where W_t is the final weight in grams, W_o is the initial weight in grams, G_S = average daily temperature in ° C/1,000, and t = days reared at the average temperature	GS	Iwama and Tautz 1981, data reported in the literature were used to derive the equation	By rearranging the equation, the estimated time to raise a fish of a specified size (g) to a larger size can be predicted: $t = \text{days} = \frac{W_t 0.33 - W_o 0.33}{G_S}$ Also, the average daily temperature required to raise a fish to a larger size in a specified time (t in days) can be estimated: T = average daily temperature (° C) = $G_S \times 1{,}000$ where $G_S = \frac{W_t 0.33 - W_o 0.33}{t}$ The equations were developed for hatchery conditions for salmonids, including brown trout; 4 to 18° C was the range for normal operations
Brown trout from the 1939 and 1940 year classes from a New Zealand stream grew more rapidly below 13° C than fish from Britain, and the growth for New Zealand trout was also greater in the 13 to 19.5° C range	E	Allen (1985), wild fish from stock introduced in New Zealand in 1868	Allen compared his results with those from experiments of Elliott (1975a, 1975b) with fish from Britain. Allen thought that the New Zealand trout grew when temperatures exceeded 19.5° C. This was the reported limit for growth for British fish. It is uncertain if differences for the New Zealand fish were genetically caused. The difference may have been caused by feeding conditions because the British fish were held under laboratory conditions
Maximum growth was at 14.9° C	F	Jensen (1990), Norwegian rivers	Actual growth was compared with predicted growth using Elliott's (1975a) model for excess rations, which was applicable to constant and fluctuating temperatures. Actual growth in 12 streams was between 76% and 136% of predicted growth. In autumn the growth rate was lower than in spring at the same temperature; causes were possibly from diminished availability of aquatic insects and a decreased rate of feeding in autumn

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
Equation for estimating growth in weight $W_t = [b_1(a + b_2T)t + W_0^{b_1}]^{1/b}$ where W_t = final weight in grams, W_0 = initial weight in grams, t = time lapse in days, T = temperature in ° C assumed to be appropriate for average conditions, and a, b_1, b_2 = constants	E	Elliott (1975a), Pickering, Yorkshire hatchery in England	The equation is for maximum rations for brown trout weighing 5–300 g and temperatures of 3.8 to 19.5° C. Values for the constants are as follows: ° C range / a / b_1 / b_2 3.8–12.8 / −0.0100 / 0.3250 / 0.0029 13.6–19.5 / 0.0820 / 0.2917 / 0.0042 The equation seemed suitable for application to wild and hatchery fish for various foods. W_t is for theoretical conditions. The growth rate (G_W% day^{-1}) was greatest at 12.8–13.6° C. The equation for W_t was applicable for constant and fluctuating temperatures
Optimal temperatures for maximum growth rates were 10 to 15.5° C	GS	Jobling (1981), reported from the literature	The author reported that the growth optimum and final preferendum temperatures correlate, that is, Y = 1.05X–0.53 where X = the growth optimum, and Y = the final preferendum r = 0.937
Fishing			
Within the range of temperatures in which fishing occurred (about 8 to 25° C) catch rates tended to diminish with increasing temperatures	E	McMichael and Kaya (1991), Madison River, Montana	At temperatures of about 19° C and higher, unsatisfactory catch rates occurred
Selection temperature			
The modal temperatures selected on an annual basis for adults was 12° C when ambient Lake Michigan temperatures ranged from 1 to 17° C and discharge temperatures ranged from 11 to 31° C	E	Spigarelli et al. (1983), Point Beach Nuclear Power Plant discharge. Two Creeks, Lake Michigan	In late summer, tagged females selected 18° C, and tagged males selected 15° C. In October males selected 18° C compared with 12° C for females
When mean daily summer temperatures exceeded 24° C, or the daily maximum exceeded 25° C, cooler temperatures were sought	F	Kaya et al. (1977a), Firehole River in Yellowstone National Park	Geothermal waters caused temperatures to rise 12° C. During hot periods trout entered Sentinel Creek, which had temperatures 6 to 10° C lower than the Firehole River
Selected 18 to 19° C in winter and 16° C in summer	F and E	Nyman (1975), Stenugsund Power Station Outlet, Sweden	Fish sizes ranged from 31 to 44 mm, and fish were tracked with ultrasonic tags
Preferred temperature minimum was 10.3° C at	E	Reynolds and Casterlin (1979), wild trout	The 24-h mean preference was 12.2° C. The range of accessible temperatures

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
1400 h. Maximum temperature was 13.7° C between 2200 and 2300 h		in Pennsylvania	was 0 to 35° C. Feeding was not permitted during the experiments
Response to exposure temperatures			
Exposing fertilized eggs to heat shock of 29° C for 10 min from 5 to 45 min after fertilization resulted in 77–91% triploid embryos	E	Arai and Wilkins (1987), the trout were from a hatchery in Parteen, Ireland	After experimental treatments, eggs were incubated at 3.5 to 9.0° C. Triploidy was 91% when the heat shock exposure lasted for 15 min
In summer, fingerlings survived for 10 days at temperatures exceeding 25° C and for 3 days at temperatures exceeding 26.7° C	E	Embody (1921), hatchery fish at the Cornell University experimental hatchery	Seventy-five fingerlings were stocked in June, and counts were made the following April; there were 37 survivors. In July and August, temperatures ranged from 20.6 to 27.5° C. The author reported the limiting factor for brown trout in streams is 28.3° C, and I interpret this to mean an exposure temperature of short duration. Information regarding how long the trout could tolerate the temperature was not stated. However, in an experiment in which temperatures rose to 27.1° C and increased to 29.7° C, in 5 days there was 50% mortality. One day later the temperatures rose to 30.6° C, and all of the trout died. The preceding information was presented as a paper. In notes from a discussion following the presentation, one commentor stated that it would be unwise to try to propagate trout where temperatures would be 21.1 to 23.3° C for a month
The critical thermal maximum (CTM) was 28.96 ± 0.41° C for a 10° C acclimation compared with 29.85 ± 0.58° C for a 20° C acclimation	E	Lee and Rinne (1980), Ord Creek, Arizona	CTM was defined as the exposure temperature at which a fish loses its ability to escape lethal conditions. The fish were 15–20 cm in total length and were acclimated for 2 weeks. During the experiment, temperatures were increased at the rate of 0.02° C/min
Number of circuli and the rate of circuli formation were higher for fry incubated at 7° C compared with 2° C	E	Skurdal and Anderson (1985), Norway	Eggs and alevins were incubated at temperatures of 2 and 7° C. The respective ranges in numbers of circuli for the two treatments were 2–9, and 5–14. Following the exposure period, brown trout in the 7° C treatment were reared at 3 to 5° C. Afterwards, temperatures for both treatments were

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
			the same (5 to 10° C). Because there were differences in circuli numbers for the two treatments, manipulation of incubation temperatures was recommended as a way to mark hatchery fish
Larvae tolerated 20° C for a 7-day period	E	Bishai (1959), Dove Marine Laboratory, England	The trout eggs had incubated at an average temperature of 7.5° C and were introduced into tanks of water at 6° C. The temperature was elevated to 20° C in 4–6 h. At 10 and 20° C acclimation temperatures, mortality was not observed for test temperatures of 22, 22.5, and 23° C for a 7-day period. For the same acclimation temperatures, 100% mortality occurred in 168 h at a test temperature of 24° C
Upper tolerance limits seemed to be 22.5 to 25.3° C	E	Frost and Brown (1967), assumed to be for British brown trout	Results were from exposures up to 7 days in tank experiments
Fry began to show stress at 25° C	E	Rushton (1926), British Isles fish	Within 2 h after the temperature was reached, 80% of fry died. The author recommended 25° C as a safety limit that should not be exceeded for fry
Critical range: Lower = 0–4° C Upper = 19–30° C	GS	Elliott (1981), trout source unstated	Visible thermal stress can occur in the two ranges. The lower value for the upper range approximates the avoidance, restlessness, or disturbing temperature. The higher temperature in the range is the maximum temperature at which fish can survive for brief periods
Physical response			
The Q_{10} for the relation between temperature (° C) and incubation was 4.9 for temperatures from 2 to 11° C	E	Embody (1934), New York hatchery	The Q_{10} is a rate of development, over an increment of 10° C, during incubation based on the Arrhenius (Embody 1934) equation: $Q_{10} = \frac{T_2}{T_1} \times \frac{10}{0_1 - 0_2}$ where T_1 and T_2 are days for temperatures 0_1 and 0_2, respectively
The mean rate coefficient (λ) for heat gain for brown trout = 0.11 with a range of 0.03–0.37. This compares with a mean of 13.6 and a range of 2.6 to 31.4 for heat loss	E	Spigarelli et al. (1977), Lake Michigan brown trout	The rate coefficient is a component of the equation: $T_f = (T_b + T_o - T_b)e^{-\lambda t}$ where T_f = instantaneous body temperature at any time, T_b = exposure temperature (° C) at time t, T_o = initial body temperature (° C), and T = time of exposure in minutes

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
			The mathematical expression for λ is: $-\ln \frac{(T_f - T_b)}{T_o - T_b} \div t$ The equation for $t_{1/2}$, the time required for half the heating to occur is $\log t_{1/2} = -0.10 + 0.70 \log wt$, and for cooling it is $\log t_{1/2} = -0.56 + 0.50 \log wt$. On a log-log plot, $t_{1/2}$ in minutes is directly proportional to wt in g, the independent variable
Mean freezing temperature of brown trout was −0.81° C ± 0.022 SE	E	Fletcher et al. (1988), streams near Bay Bulls Big Pond, Newfoundland	The freezing temperature was designated when brown trout exhibited convulsions. They died unless they were transferred to water >0.5° C. The mean weight of the experimental fish was 252 ± 33 g (SE). The freezing temperature was less than the plasma freezing temperature, which suggests that there is some "antifreeze" component to account for the difference
In the 9.4 to 20.5° C range, the following equation pertains to the mean O_2 concentration (Y) in ppm that is lethal $\log Y = 0.01248X - 0.46056$ where X = temperature (° F)	F	Burdick et al. (1954), fish from the Rome, New York, hatchery	The fish were yearlings
Habitat quality-related			
Fry of two sizes (32 and 43 mm total length) preferred gravel in the 50- to 70-mm range in two experiments of 12.9 to 18.1° C and 6.0 to 6.9° C	E	Heggenes (1988), NIVA fish hatchery, Norway	Fry could choose between three size classes of gravel (8–16, 20–30, and 50–70 mm). Experiments were in artificial stream channels. Fry hide in substrate more in the daytime and at low temperatures. The degree of preference for substrate size was influenced by fry size, water temperature, night versus day, and water velocities. Smaller fish (32 mm) had a weaker preference for the coarse substrate and generally had fewer diurnal preferences
Stream rating for maximum summer temperatures (° C)	E	Binns and Eiserman (1979), data from Wyoming streams	Maximum summer temperature was one of nine variables in a multiple regression model for predicting standing crop for four fish species, including brown trout

Stream rating

0 (worst)	1	2	3	4 (best)
<6 or >26.4	6–8 or 24.2–26.3	8.1–10.3 or 21.5–24.1	10.4–12.5 or 18.7–21.4	12.6–18.6

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
Maximum average summer temperatures of water should be near 18.9° C, with maximum short-term temperatures less than 22.8 to 23.9° C	GS	Tebo (1974), general observations from the literature	The author cited data for six states for which 20° C was stipulated as the allowable maximum except for one state (North Carolina), where the maximum was 21.7° C for put-and-take waters. The information is for trout in general
Optimum water temperature was 18.3 to 23.9° C	N	Mansell (1966), Ontario streams	For the best streams, the range was 11.7–22.8° C, and temperatures never exceeded 27.2° C
Survived temperatures up to 27.2° C	GS	Needham (1969), general statement	The author specified the value as the highest limiting water temperature. The time of tolerable exposure was unstated
Activity and feeding			
Brown trout were caught in O° C water, and they were active throughout the winter	E	Maciolek and Needham (1952), Convict Creek, California	Surface feeding was observed when aerial insects were present at temperatures of 1.7–5.6° C. At least 50% of the food fed to fish in an experiment was digested in 14 h at temperatures ranging from 0 to 1.7° C. Brown trout were reluctant to migrate at temperatures below 5.6° C
Brown trout were most active between 18.3 and 23.9° C	GS	Brynildson et al. (1963), observation for Wisconsin	At 20° C, the minimum tolerated dissolved oxygen concentration was 5 ppm. At lower temperatures, lower concentrations could be tolerated
Appetite was maximum between 10 and 19° C	E	Frost and Brown (1967), British Isles fish	Appetite fell off sharply outside the range. Results were for fish maintained in tanks
Appetite was maximum between 13.3 and 18.4° C	E	Elliott (1975c), British Isles hatchery fish	Relatively constant treatment temperatures ranged from 3.8 to 21.6° C. Most trout readily fed at 6–19° C. They were inactive yet reluctant to feed at <6° C and were active and reluctant to feed above 19° C. Trout in the experiments ranged from 1 to 300 g
The maximum rate of feeding increased from 3.8 to 6.8° C, remained fairly constant in the 6.8 to 19.3° C range, and decreased markedly above 19.3° C	E	Elliott (1975d), assumed to be British Isles hatchery fish	The equation: $$N = \frac{(24)}{a} e^{bT} = Ae^{bT}$$ is the expression for the number of meals (N) per day where a, A, and b are constants and T is temperature (° C). The maximum weight (mg dry weight) of food consumed per meal (Q) is represented by $Q = aW^{b_1}e^{b_2T}$ where a, b_1, and b_2 are constants, W = live weight of trout in grams, and T = temperature (° C). The maximum weight of food (mg dry weight) consumed per day = $D = A_DW^{b_1}e^{b_2T}$ where A_D, b_1, and b_2 are constants, and T = temperature (° C). The experimental food was dried *Gammarus*

Table 1. *Continued.*

Attribute	Observation[a]	Reference and fish source	Comments
The relation between rate of feeding (F) and water temperature (T in ° C) was $F = \log e^C + dT$ where c and d are constants	E	Elliott (1975d), assumed to be British Isles hatchery fish	The value of F increased rapidly from 3.8 to 6.8° C and remained relatively constant to 19.3° C, when it declined. The author stated that the equation was suitable for a wide variety of experimental food items
Shore fishing success for stocked fish declined at temperatures >18° C	F	Taylor (1978), Eye Brook, Leicestershire	Apparently the brown trout sought out cooler water in addition to having reduced appetite
Feeding rate optimal at 7 to 19° C	E	Elliott (1981), assumed to be British Isles trout	The optimum range was 13–18° C for voluntary food intake and satiation time for 50-g (live weight) British Isles trout

[a] GS = general statement; F = natural field conditions; E = experimental.

Table 2. Data for brown trout for selected responses to experimental temperatures.

Attribute	Comment
Upper ultimate incipient lethal temperature (UUILT) was >29° C[a]	Calculations of UUILT from Jobling's (1981) equations results in a value of 28.0° C for a final preferendum (FP) of 17.6° C compared with 26.3° C for a growth optimum (GO) of 16.4° C
UUILT was 25 to 30° C[b]	Assumed to apply to brown trout 10–25 cm long and 10–185 g. Survival was 10 min for acclimation temperature of 0–27.5° C
Critical thermal maximum (CTM) = 28.96° C for 10° C acclimation and 29.76° C for 20° C acclimation[c]	The values represent median temperatures for equilibrium loss
Growth optimum (GO) = 16.4° C[a]	The author listed a range of 10 to 21° C for different diets, life stages, and seasons
Zero net gain (ZNG) ranges: Lower: <2.0 to 3.8° C Upper: 19.5 to >21.2° C[a]	ZNG is defined as conditions when instantaneous growth and mortality rates for populations are equal. This is when increases in biomass of surviving individuals are offset by losses in biomass from mortality
Physiological optimum (PO) = 17.0° C[a]	Physiological optimum is defined as the temperature under experimental conditions approximating that for optimum growth, heart performance, and other physiological functions
Final preferendum (FP) = 12.4–20.0° C[a]	The author also listed 17.6° C as a single value. Cherry et al. (1977) reported a range of 12.0 to 17.8° C from literature sources. Ferguson (1958) reported a range of 12.4 to 17.6° C from the literature

Acclimation temperature (° C)	Regression coefficients a	Regression coefficients b	Comment
6	36.1429	−1.4286	The data are for juvenile brown trout. Data for fry and smolts are in the same source
15	21.5714	−0.7143	
20	17.6667	−0.5556[d]	

[a] Hokanson (1990a).
[b] Elliott (1981).
[c] Lee and Rinne (1980).
[d] Brungs and Jones (1977).

Table 3. Temperature and egg development relations for brown trout for alternative temperature regimes.

Variable	Alternative temperature regime A	B	C
Temperature range (° C)	6–11	1.5–11	4–17
Average temperature (° C)	10.8	4.0	12.0
Estimated egg mortality (%)	40[a]	24	80
Estimated days till hatching	36[b]	104	<34

[a] Value obtained from Fig. 2 for the average temperature of 10.8° C.
[b] Value obtained from Fig. 3 for the average temperature of 10.8° C.

requirements are acceptable. Also, assume that the temperature range of 2.8–13° C (Table 1; Gray 1928) is acceptable for incubation. Alternatives A and B should suffice; however, if egg mortality is a concern, alternative B, with an estimated mortality rate of 24% (Fig. 2), would be preferable. Also, days until hatching could be estimated from experimental results (Fig. 3). Because brown trout are fall spawners, a decision would be needed about the preferability of alternative B over A regarding time of hatching. For example, there could be a problem with synchronization of food availability for alternative A because after 36 days midwinter hatching would be predicted.

Growth might be another concern. Variables affecting brown trout growth fall into physicochemical and biotic categories (Wingfield 1940). In the first category, water temperature and water chemistry are probably most important; in the second, food availability seems to be most important (Wingfield 1940). From a growth potential perspective, I hypothesize that results from temperature experiments would be most useful in comparing alternative temperature regimes. Reliance on experimental data, however, should be confined to theoretical rankings. Accordingly, if an alternative is ranked higher than another, the distinction would be qualitative. For spawning and egg incubation success, which are more directly linked to temperatures than to biotic factors, assuming that all other habitat criteria are met, there would be a higher probability that reproductive success in the field would resemble results from temperature experiments.

Another example involves the use of Elliott's (1975a) equation (equation 1) for final weights. If Elliott's equation were used to evaluate the alternative temperature regimes in Table 4, the inter-

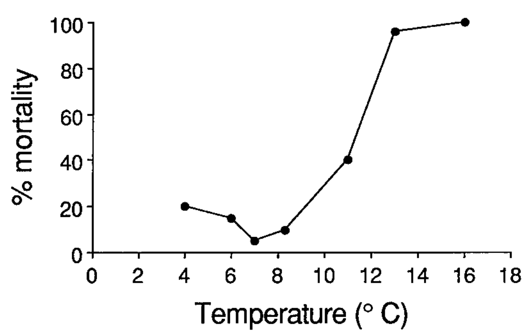

Fig. 2. Relation between constant incubation temperatures and mortality rates for brown trout eggs (Jungsworth and Winkler 1984). A similar relation is assumed to apply for average temperatures during incubation.

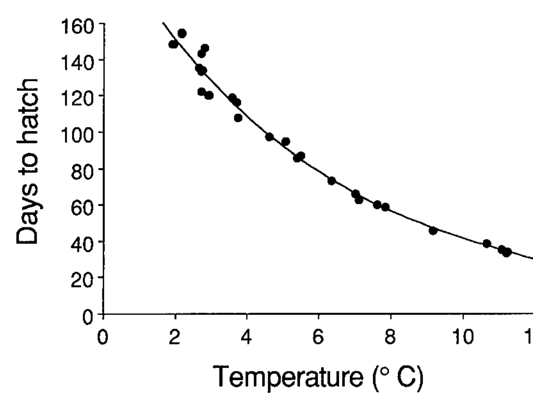

Fig. 3. Relation between mean incubation temperatures and hatching days for brown trout (Embody 1934).

Table 4. Final weights of brown trout for alternative flow regimes.

Variable	Alternative flow regime A	B
Average temperature (° C)	10	13
Initial weight (W_o) in grams	10	10
Growth period (days)	45	50
a	−0.0100	0.0820
b_1	0.3250	0.2917
b_2	0.0029	−0.0042
Final weight (W_t)[a] in grams	14.6	18.9

[a] $W_t = [(b_1(a + b_2T)t + W_o^{b_1}]^{1/b_1}$
$= [0.3250((-0.01 + (0.0029)10))45 + 10^{0.3250}]^{1/0.3250}$
$= [0.27788 + 10^{0.3250}]^{3.07692}$
$= 2.39137^{3.07692}$
$=$ antilog 3.07692 log 2.39137
$=$ antilog 1.165076 = 14.6 g

pretation of results would be that, from a theoretical perspective, regime B provides more potential for growth.

$$W_t = [b_1\ (a + b_2\ T)t + W_o^{\,b_1}]^{1/b_1} \qquad (1)$$

where

W_t = final weight (g); a, b_1, and b_2 are constants;
T = average temperature (° C); and
W_o = initial weight (g).

Site-specific growth responses could differ from those predicted from the equation because it was derived for experimental conditions with maximum rations. Another possibility would be to use Iwama and Tautz's (1981) equation (equation 2) to evaluate the theoretical time required for a brown trout to attain a designated weight for alternative temperature regimes (Table 5). This method requires use of average temperatures during a prescribed period

Table 5. Ranking of alternatives according to the least time required for a 15-g brown trout to attain 100 g.

Variable	Alternative temperature regime A	B	C
Average temperature (° C)	5	7	13
Initial weight (W_o) in grams	15	15	15
Final weight (W_t) in grams	100	100	100
G_s = ° C/1,000	0.005	0.007	0.013
Days to attain W_t	425[a]	304	164
Rank	3	2	1

[a]
$$t = \frac{W_t^{\,0.33} - W_o^{\,0.33}}{G_s} = \frac{100^{0.33} - 15^{0.33}}{0.005}$$
$$= \frac{\text{antilog } 0.33 \log 100 - \text{antilog } 0.33 \log 15}{0.005}$$
$$= \frac{\text{antilog } 0.66 - \text{antilog } 0.3881}{0.005}$$
$$= \frac{4.5709 - 2.4440}{0.005}$$
$$= \frac{2.1269}{0.005} = 425 \text{ days}$$

(e.g., a summer growing season). Alternative C, with 164 days, would be ranked first. Because the equation was derived for hatchery conditions, with maximum rations, the times estimated to attain a designated weight would be relative.

$$t = \frac{W_t^{\,0.33} - W_o^{\,0.33}}{G_s} \qquad (2)$$

where

t = estimated time in days to attain a specified weight,
W_t = designated final weight (g),
W_o = initial weight (g), and
G_s = average temperature in ° C/1,000.

An option would be to use a modified form of Iwama and Tautz's (1981) equation (equation 3) and to solve for T (° C)—the average theoretical temperature (i.e., $T = G_s \times 1{,}000$).

$$G_s = \frac{W_t^{\,0.33} - W_o^{\,0.33}}{t} \qquad (3)$$

where

t = time in days (e.g., length of growing season).
Other expressions are the same as in equation 2.

Alternatives would be ranked relative to the theoretical temperature required to attain a specified weight in a designated period (Table 6). For example, alternative A, with an average temperature of 13° C for the 180-day period, would rank first. The approach would not be restricted to alternatives with equal growing seasons. However, for alternatives with different lengths of growing season, the criterion would have to be the ultimate weight—not the shortest period for its attainment.

When temperatures are simulated for alternative regimes, ranges of predicted temperatures should be used instead of averages because averaging can result in failure to consider harmful temperatures outside of tolerance limits.

General Considerations

Ideally, evaluating temperature regimes for fish species should be a "cookbook" process. For the foreseeable future, however, such studies will rely on existing information and professional judgment, which emphasizes the need for a sound problem analysis process (Fig. 4) for studies. Prior to proceeding from one step to another in the problem analysis process, the rationale for decisions should be carefully documented, for two reasons. First, the thought processes for decisions will be available to all concerned with a project. Second, because the

Table 6. Ranking of alternative temperature regimes for proximity of the average daily temperature to a theoretical temperature for attainment of 15-g brown trout to 100 g in 180 days.

Variable	Alternative temperature regime A	B	C	D
Time (t) in days for growing season	180	180	180	180
Final weight (W_t) in grams	100	100	100	100
Initial weight (W_o) in grams	15	15	15	15
G_sa	0.0118[a]	0.0118	0.0118	0.0118
Average daily temperature (° C)	13	17	16	14
Theoretical temperature (T ° C)	11.8[b]	11.8	11.8	11.8
Rank	1	4	3	2

[a] G_s = Average daily temperature (° C)/1,000

$$= \frac{W_t^{\,0.33} - W_o^{\,0.33}}{t}$$

$$= \frac{\text{antilog } 0.33 \log 100 - \text{antilog } 0.33 \log 15}{180}$$

$$= \frac{4.5709 - 2.4440}{180} = \frac{2.1269}{180} = 0.0118$$

[b] $T = G_s \times 1{,}000 = 11.8$

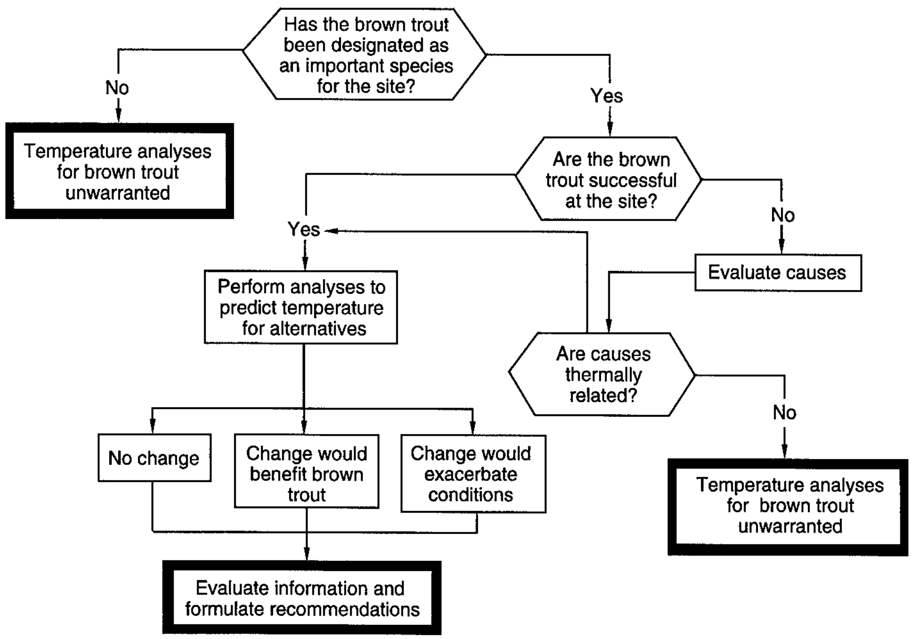

Fig. 4. Flowchart for the temperature analysis process.

rationale for the entire process is documented, the probability of resolving conflicts with those who might interpret information differently will be enhanced.

A special challenge will be to account for water quality problems that temperatures might exacerbate, for example, at a site where alternative flows are proposed but a toxicant is present. Temperature alterations in either direction may cause an increase, decrease, or no change in toxicity for aquatic organisms, depending on the toxicant (Rand and Petrocelli 1985). For some toxicants, there is a relation between concentration and decreased ability of fish to withstand thermal stress. Channel catfish (*Ictalurus punctatus*), for example, exhibit an inverse relation between critical thermal maxima and concentration of nitrite; as nitrite increases, the oxygen binding capacity of methemoglobin decreases to cause methemoglobinemia (Watenpaugh and Beitinger 1985). Figure 5 shows the effects of nickel on rainbow trout temperature tolerance. The time to loss of equilibrium decreases as concentration of the toxicant increases even though water temperatures are lower.

It exceeds the scope of this report to discuss details about effects of toxicants in conjunction with temperatures. Suggested sources of basic water quality information include the National Academy of Sciences and Engineering (1972) "blue book" and the U.S. Environmental Protection Agency (1976) "red book." Information relevant to water quality and fish kills can be found in the U.S. Fish and Wildlife Service (1990).

Short-term extreme temperatures and exposure periods are important considerations when evalu-

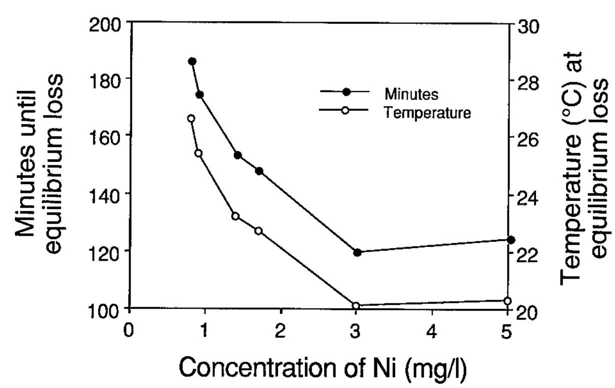

Fig. 5. Relation between time of equilibrium loss and temperature at different nickel concentrations for rainbow trout (*Oncorhynchus mykiss*; Becker and Wolford 1980).

ating alternative temperature regimes (Brungs and Jones 1977; Armour 1991) because tolerance to temperatures depends on acclimation temperatures and the magnitude and duration of exposure periods. Short-term temperature tolerance information might be unavailable for a particular life stage. In this case, assume that any temperature, regardless of the exposure time, outside the range observed for successful populations would be detrimental.

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